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Abstract

Estimating abundance of downstream migrants in anadromous salmonid populations typically relies on trapping a portion of the population as it passes a fixed point on a stream and expanding this count using capture probabilities estimated with mark-recapture techniques. Numerous factors cause the probability that an individual passing the trap will be captured to vary over time, and such variation, if not accommodated in the analysis, can seriously bias the resulting estimate of abundance. Likewise, substantial time intervals between the release of marked fish and their subsequent susceptibility to recapture can bias abundance estimates if such intervals are not measurable and accounted for in the analysis. Stratified mark-recapture experiments, in which marks applied to individuals are changed over time so that recaptured individuals can be assigned to the period in which they were released and recaptured, allow the use of statistical estimators that explicitly accommodate variation in capture probability and the distribution of marked individuals among the sampling periods or strata. However, issues related to small sample sizes can hinder the application of such estimators in small populations, particularly in cases where time intervals between release and recapture can be substantial; such conditions are commonly observed in populations of coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) in small coastal streams. DARR 2.0 updates a software application for estimating abundance from stratified mark-recapture data sets. DARR 2.0 applies a series of algorithms to a stratified mark-recapture data set to aggregate strata as necessary to yield an admissible estimate of abundance (using the Darroch (1961) stratified-Petersen estimator) while preserving as much structure as possible in the data. This software is provided to encourage and support the use of statistically rigorous abundance estimators in monitoring programs that focus on estimating the abundance of downstream migrants in populations of anadromous salmonids, but may also be used to analyze other temporally or spatially stratified mark-recapture data sets in which the number of tagging and recapture periods are equal.

Introduction

DARR (Darroch Analysis with Rank Reduction) 2.0 updates¹ a software application for estimating abundance from stratified mark-recapture data. The development of this software is motivated by the need for rigorous estimates of the production of smolts (or more correctly “downstream migrants”) in populations of salmon and steelhead, and the necessity to overcome common difficulties that limit the application of mark-recapture estimators in small watersheds. The software itself is more general, however, and can be used to estimate abundance whenever the stratified mark-recapture design includes an equal number of tagging and recapture strata, and is thus amenable to analysis with the Darroch (1961) estimator².

Estimating abundance of downstream migrants typically involves trapping downstream migrants at a fixed location over time. Where a census is impossible or impractical, mark-recapture techniques are used to estimate the probability that an individual will be captured (i.e., “trap efficiency”), which in turn is used to expand counts of captured individuals to produce an estimate of total abundance.

Mark-recapture estimators generally entail a number of assumptions (Schwarz and Taylor, 1998), including: (1) that the population is closed (i.e., that all marked individuals are susceptible to recapture during a recapture stratum), or that both marked and unmarked individuals die or emigrate at the same rates; (2) that marked and unmarked individuals are well-mixed in the population when the recovery sample is taken, or equivalently, that all individuals susceptible to capture when a recovery sample is taken have equal probability of being captured; and (3) that marks are not lost, that is, marks are retained for the duration of the experiment and marked individuals are unambiguously identified. The first assumption is violated if marked individuals suffer greater mortality than unmarked individuals due to a tagging effect, but if this effect is estimated externally to the mark-recapture experiment, suitable corrections can be

made.

Violations of these assumptions are typically difficult or impossible to detect or correct after the fact, and it is therefore imperative that the experimenter attempt to minimize the degree to which the experiment fails to meet these assumptions. In particular, field programs designed to estimate smolt abundance must, in most cases, accommodate temporal variation in capture probability that can seriously bias simple abundance estimators (Seber, 1982; Arnason et al., 1996; Schwarz and Taylor, 1998). Capture probability can vary over time as a consequence of variable flow conditions that affect trap performance, changes in the composition or characteristics of the population during the migration season, seasonal changes in individual behavior, or changes in trap operation (Schwarz and Dempson, 1994; Polos, 1997; Plante et al., 1998).

Stratified mark-recapture estimators provide a means of accommodating variability in capture probability explicitly and thus reducing the consequences of variability for the accuracy of the abundance estimate. Stratified mark-recapture data consist of the numbers of marked individuals released during individual tagging periods and the numbers of marked and unmarked individuals captured during individual recovery periods. Thus, the sampling season is decomposed into a series of periods or strata. It is critical that a series of “unique” stratum-specific marks be used over the course of the sampling season so that recaptured individuals can be differentiated according to the tagging period in which they were released. Otherwise, the accuracy of resulting abundance estimates can be seriously degraded by undetected variation among marked individuals with respect to the interval between their release and subsequent susceptibility to recapture (i.e., temporal migration). Stratified mark-recapture estimators explicitly account for the probability that individuals released during a tagging stratum will be susceptible to recapture in a given recovery stratum in the course of estimating capture probabilities (e.g., Darroch, 1961; Schwarz and Taylor, 1998, see Appendix A). Thus, such estimators provide a means of simultaneously accommodating both (1) variability in capture probability and (2) the distribution of marked individuals among recovery strata in the course of estimating total abundance.

In this report, I describe an update to software that applies Darroch’s (1961) stratified-Petersen abundance

¹The previous version of this software is described in Bjorkstedt, E. P. 2000. DARR (Darroch Analysis with Rank-Reduction): a method for analysis of stratified mark-recapture data from small populations, with application to estimating abundance of smolts from out-migrant trap data. NMFS SWFSC Administrative Report SC-00-02.

²Designs with unequal numbers of tagging and recapture strata require analysis using numerical methods not implemented in DARR 2.0 (e.g., SPAS at <http://www.cs.umanitoba.ca/~popan/>).

estimator to mark-recapture data collected from small populations in which marked individuals may be at-large for substantial intervals of time between release and susceptibility to recapture. The software comprises a series of algorithms that aggregate the mark-recapture data to the degree necessary for analysis, and then applies the (Darroch, 1961) estimator. In some cases, goodness-of-fit tests can be used to evaluate whether aggregated data will continue to satisfy the assumptions of an estimator, and thus guide decisions regarding how to pool data to obtain a more parsimonious estimator (Darroch, 1961; Schwarz and Taylor, 1998). However, in many cases application of such tests to data collected from a small population or tag-group will have unsatisfactory power or perhaps will be impossible to execute due to small sample size (Schwarz and Taylor, 1998). In such cases, it may be necessary to aggregate the data without the benefit of solid statistical guidance on whether and how to do so. DARR 2.0 accomplishes this by sequentially applying a series of rules to pool coincident tagging and recovery strata based on the structure of the data, with the goal of achieving an admissible estimate that includes minimal bias while maintaining as much of the structure in the data as possible.

The main body of this report highlights changes in the updated software and provides a users' manual for DARR 2.0. Appendices to this report provide details regarding (1) stratified mark-recapture data, estimators and conditions under which estimators fail or perform poorly, (2) the full sequence of updated rules for identifying structures in the data that hinder or prevent analysis, and (3) the algorithm for eliminating such structures by aggregating strata and the consequences of doing so for model structure and assumptions. Much of the material in Appendices A and C has been presented previously in an Administrative Report associated with earlier versions of DARR, and is included here for the reader's convenience.

Changes implemented in DARR 2.0

DARR 2.0 includes numerous updates from previous versions of DARR. Some of the changes are cosmetic or simply extend the functionality of the software; these are noted below, and are treated in more detail in the users' manual that follows. More importantly, DARR 2.0 also includes three small, but significant, changes

to the pooling algorithm used to aggregate data prior to estimation (described below; and in more detail in Appendix B). Analysis of simulated data indicates that the new algorithm improves the performance in the estimator (i.e., reduces bias and decreases sensitivity of estimator behavior to details of the underlying mark-recapture process; E. P. Bjorkstedt *in prep.*). For a given data set, differences in the estimates of abundance provided by different versions of DARR are expected to be small, and indeed, estimated abundance may not change. Regardless, it is recommended that data analyzed with previous versions of DARR be re-analyzed with DARR 2.0. Backward compatibility has been maintained, so that data sets analyzed with previous versions of DARR do not require reformatting for analysis with DARR 2.0.

Changes to algorithm

The first change implemented in DARR 2.0 ensures that the analysis is not artificially compromised by consistently long intervals between marked individuals' release and susceptibility to recapture. If at-large intervals are long relative to the stratification interval, few "immediate" recaptures will be observed, and the aggregation algorithms will tend to overaggregate the data. Therefore, in contrast to previous versions, DARR 2.0 ensures that \mathbf{R} has a dominant main diagonal prior to determining whether the data require further aggregation for analysis. To accomplish this, DARR 2.0 first determines whether \mathbf{R} has a dominant main diagonal, and if not, shifts recaptures and unmarked captures "forward" in time so that the resulting \mathbf{R} does have a dominant main diagonal. This shift is corrected in presentation of the final results. In most small-scale downstream migrant trapping programs, the bulk of marked individuals typically are susceptible to capture soon after release, and the resulting recapture data exhibit a dominant main diagonal; therefore, this change is likely to have no effect in most cases.

The second change implemented in DARR 2.0 is a dynamic definition for the critical threshold for condition number of \mathbf{R} used to determine whether aggregation should occur. Step 3 of the pooling algorithm in DARR 2.0 (step 2 in previous versions) no longer includes a fixed critical value for the condition number of \mathbf{R} . Instead, the threshold is now set by the average number of (non-zero) "immediate" recaptures. In pre-

vious versions of DARR, the fixed threshold tended to cause more aggregation of data that included many recaptures and less aggregation of data with few recaptures. The new, dynamic threshold reduces the sensitivity of estimator behavior to changes in total abundance, and thus reduces the potential for estimator-related bias when evaluating trends in abundance (E. P. Bjorkstedt, in prep.).

The third change is in how strata are selected for aggregation in Step 3 (Step 2 in previous versions of DARR). In previous versions of DARR, the pair of strata that, when aggregated according to the pooling algorithm, yielded the greatest reduction in the condition number of \mathbf{R} was selected for aggregation. In DARR 2.0, this criterion is modified so that the strata that yields the greatest reduction in the condition number of \mathbf{R} as a consequence of increasing the minimum singular value of \mathbf{R} is selected (See Appendix B). This criterion favors aggregation of strata with few recaptures over those with many.

Changes in operation

Users of previous versions of DARR will notice substantial differences in the appearance of the Graphical User Interface (GUI), which has been redesigned to take advantage of dialog utilities available in MATLAB (The MathWorks, Inc. <http://www.mathworks.com>). These differences are generally cosmetic, but also afford greater flexibility in implementing the underlying analysis.

Four changes have been made to extend the utility of DARR 2.0 beyond that of previous versions. First, DARR 2.0 accommodates data sets that include arbitrary numbers of strata. Very large data sets may overwhelm the ability of DARR 2.0 to display data in tabular form, but the analytical machinery is not compromised. Second, DARR 2.0 allows the analyst to select contiguous series of strata to be pooled prior to application of the automatic pooling algorithms. Third, file management has been extended to allow the reading and writing (saving) of data in space-delimited (.txt) and comma-delimited (.csv) formats. The latter format is recommended as it can be read directly by spreadsheet applications. Fourth, DARR 2.0 provides the analyst multiple options for the printing or saving of graphical output from analysis, including direct printing, saving the image to the clipboard for subsequent pasting into a docu-

ment, or saving the image in any of a suite of graphical formats.

Note that DARR 2.0 no longer explicitly supports data entry and management. It is still possible to edit data in DARR 2.0 if, say, a typographical error is noticed during analysis, but it is strongly recommended that all data preparation and initial stratification be conducted in a spreadsheet or database application.

DARR 2.0 Users' Guide

DARR 2.0 implements the algorithms and estimator described in this report to analyze stratified mark-recapture data sets. The software was developed in MATLAB 6.5 (The MathWorks, Inc. <http://www.mathworks.com>) and compiled into a standalone application for Windows PC (32-bit MS-DOS console application) using the MATLAB C/C++ Compiler Suite 3.0 and Microsoft Visual C++ 6.0.

Obtaining and installing DARR

Software to install DARR 2.0 can be downloaded from the Santa Cruz Laboratory web page³. The software (including necessary support files) and an example data set are included in the self-extracting WinZip⁴ file DARRv2.Distribution.exe. This file is approximately 9 MB in size, and expands to a folder approximately 25 MB in size.

To install DARR 2.0, run the self-extracting file (DARRv2.Distribution.exe), and follow the prompts to choose (or create) a directory (folder) where DARR 2.0 will reside. Running the self-extracting file creates a folder named 'DARRv2' in the selected directory. This directory contains DARRv2.exe, DARRExample-Data.csv, a handful of other files, and two subdirectories, '\bin' and '\toolbox', which contain the necessary files to allow DARR 2.0 to run on a machine on which MATLAB is not installed. **It is recommended that DARRv2.Distribution.exe be run in the directory in which mark-recapture data are stored.** For example, if mark-recapture data is stored in 'C:\Smolt\MarkRecap', running DARRv2-zip.exe in this directory will create 'C:\Smolt\MarkRecap\DARRv2'. File management and directory navigation during the course

³<http://santacruz.nmfs.noaa.gov/publications/software/439/>

⁴WinZip (<http://www.winzip.com/>) software is *not* necessary to open this file

of analysis will be more convenient if the executable file DARRv2.exe is moved (or copied) to the data folder, but this is not necessary. To enable DARR 2.0 to run successfully, it is necessary to append the subdirectory '<DARRv2 directory>\bin\win32' to the system path variable (PATH)⁵. No changes are made to the operating system's registry, and uninstalling DARR 2.0 is as simple as deleting the directory containing installed files (e.g., 'C:\Smolt\MarkRecap\DARRv2') and removing the appended entry from the PATH.

How to use DARR 2.0

Data preparation

Data should be stratified appropriately with respect to the marking scheme prior to analysis. For example, a mark-recapture experiment in which the mark is changed every 7 days will require stratification at 7 day intervals even though data are collected on a daily schedule. Stratification is most easily handled in a spreadsheet application.

Data to be imported to DARR 2.0 should consist of a row for each release stratum, each of which contains, in order, an entry for the number of newly captured (unmarked) individuals (u_j , $j = 1, 2, \dots, t$), an entry for the number of marked individuals released (m_i , $i = 1, 2, \dots, s$), and a series of entries for the number of recaptures from that mark group for each sampling period (r_{ij} , including necessary zeros). The data should be arranged as

$$\begin{array}{ccccccc} u_1 & m_1 & r_{11} & r_{12} & \cdots & r_{1t} & \\ u_2 & m_2 & (r_{21}) & r_{22} & & r_{2t} & \\ \vdots & \vdots & \vdots & & \ddots & \vdots & \\ u_t & m_s & (r_{st}) & \cdots & (r_{s,t-1}) & r_{st} & \end{array} \quad (1)$$

noting that the number of release and recapture strata must be equal, i.e., $s = t$, so that the recapture portion of the data is a square matrix. The parenthetical entries

⁵Go to Control Panel–System–Advanced–Environment Variables. Select "Path" in the lower window and click on "edit". **Do not write over the existing PATH!** Instead, append the full path of the required directory to the end of the existing path. For example, if DARR 2.0 is installed in 'C:\Smolt\MarkRecap\DARRv2', append the path-name ";C:\Smolt\MarkRecap\DARRv2\bin\win32" (without quotation marks) to PATH. Note that the initial semi-colon preceding the pathname is needed to separate the new entry from the previous entry in PATH. Please consult the manual for your computer's operating system for more details.

below the main diagonal of the recapture matrix \mathbf{R} will be zeros in data collected with a downstream migrant trap or any other temporally stratified data set (a fish can not be recaptured before it was released).

Data so arranged should be saved as a comma-delimited file (e.g., data.csv) or a tab- or space-delimited ASCII file (e.g. data.txt). Most, if not all, spreadsheet applications allow data to be saved in either format. The comma-delimited format is preferred as this format is readily viewed and edited in most spreadsheets, and thus allows more seamless integration of DARR 2.0 and spreadsheet applications.

An example file is included with the software (DARRExampleData.csv). Note that only the uppermost matrix (i.e., the data arranged as in Eq (1)) is read into DARR 2.0; the remainder of the file is an example of saved output (see below). New data files need include only the uppermost matrix.

Running DARR

Running DARR 2.0 is as simple as clicking on the icon or running the executable file from "Start-Run" on the Windows Toolbar. This will invoke an MS-DOS console window⁶ and immediately display an information message. Clicking on "OK" closes the window and allows analysis to proceed.

Entering and managing data

DARR 2.0 will query the analyst for the data file to be used, and supports navigation among directories. DARR 2.0 no longer supports direct entry of data; if no data file is selected, a warning message appears, after which DARR 2.0 will exit. Once a file is selected, DARR 2.0 reads the data and displays the data as a row vector⁷ labelled "unmarked captures by stratum (\mathbf{u})", a row vector labelled "marks released by stratum (\mathbf{m})", and a matrix labelled "recaptures by stratum (\mathbf{R})".

DARR 2.0 also calculates the total number of recaptures for each mark group (summed across rows of (\mathbf{R}),

⁶Any messages returned from the program (including errors) will be displayed in this window, but for the most part, this window may be ignored. Note that DARR 2.0 also can be run by typing "DARRv2" (without quotation marks) at the command prompt in an MS-DOS window.

⁷Row vectors are used for display only. The data are retained in column vectors for analysis; see Appendix A.

but displayed as a row vector labelled “summed recaptures by mark group”), and performs a preliminary assessment of the data by comparing the number of recaptures to the number of marks released for each mark group. If more marked individuals were captured than were released, this suggests that the groups are not discrete and that the assumptions of the stratified mark-recapture model have been violated. If this occurs, DARR 2.0 will issue a warning that identifies the affected mark groups. The analyst will need to correct the original data before analysis can proceed. If this is a real occurrence in the data, i.e., not just a typographical error, it can have very important implications for interpretation of the results, as the assumptions of the stratified design have been violated.

Analysis

Once the data are checked, DARR 2.0 offers the analyst the option of aggregating strata before applying the automatic pooling algorithms. In general, this is not recommended; however, if there is support for aggregating tagging *and* recapture groups, i.e., evidence that capture probabilities were constant across the entire period, such as a statistical test (see, e.g., Schwarz and Taylor, 1998), then doing so can improve the performance of the underlying statistical estimator. Strata to be pooled *a priori* must be submitted in contiguous series, such as “2 3”, “5,6,7”, or “10-14”, with each series on a separate line.

DARR 2.0 then queries the analyst regarding the number of traps used in the experiment. If all captures and recaptures occur at the same trap, with marked fish being released upstream of the trap, the experiment has a one-trap design. Conversely, if fish are captured, marked, and released at one site, but the sample of marked and unmarked fish used for the analysis is collected at a second, downstream location, the experiment has a two-trap design. The design of the experiment determines how marked fish contribute to the final abundance estimate (see Appendix A).

Results

Results of analysis are presented in a window titled “Summary of analysis”. Information on how the original data were aggregated under the heading “original strata in each pooled stratum” and the three subsequent

fields give the final aggregated data set used to generate the abundance estimate. DARR 2.0 provides stratum-specific estimates of abundance for the aggregated data set, the standard error for each stratum-specific estimate (calculated as the square root of the variance estimated for each stratum-specific estimate of abundance), as well as the estimate of overall abundance and the standard error associated with the estimate of total abundance (calculated as the square root of the estimate of variance for total abundance). The formula used to calculate total abundance from the stratum-specific estimates depends on whether one or two traps are used to sample the population (Appendix A). Therefore, for clarity, the appropriate calculation is indicated in the heading of the field for the estimate of total abundance.

Note that the estimate of sampling variance of total abundance is the sum of elements of the estimated variance-covariance matrix for the stratum-specific abundance estimates (Appendix A). Negative covariance between abundance estimates for contiguous stratum-specific abundance therefore reduces the variance of the estimated total abundance. Therefore, the estimate of overall variance can be smaller than the sum of the stratum-specific variance estimates, and in some cases can be smaller than the variance estimated for a single stratum.

Results are also summarized graphically. The figure summarizes the results of analysis as follows (Figure 1). Green bars indicate the number of *unmarked* individuals captured during each period. The solid line with open circles indicates the estimates of the total number of individuals passing the recapture site during each period. If the data have been collected under a “two-trap” protocol, these estimates include the known number of marked individuals released during each period. Estimated capture probabilities are indicated by the black dotted line with “x”s. Periods aggregated *a priori* by the analyst are highlighted magenta. Periods aggregated by the algorithms implemented in DARR 2.0 are highlighted yellow.

After reviewing the tabular results, the analyst should click either button to close the tabular display. DARR 2.0 will then query the analyst whether to print or to save the figure. The options are (1) to close the figure and proceed, (2) to send the figure directly to a printer, (3) to save the figure to the “Clipboard”, whence it can

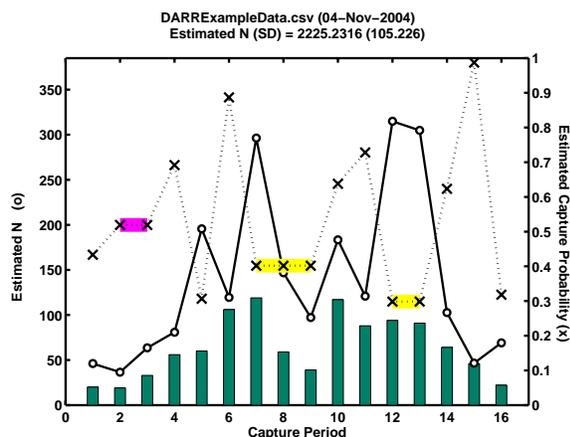


Figure 1: Graphical display of results from analysis of data provided in DARRExampleData.csv, with strata 2 and 3 aggregated *a priori* for illustrative purposes.

be pasted into a document⁸, (4) to save the figure as an Enhanced Metafile (.emf), (5) to save the figure as JPEG image (.jpg), or (6) to save the figure as an Encapsulated PostScript file (.eps). If the figure is printed or saved, the query options are again presented. To move on, the analyst must select “Close figure and proceed”.

The data needed to reproduce some or all of the figure with other graphing software are output when the results are saved (see below). Note, however, that the estimator used in DARR 2.0 is designed to yield an estimate of total abundance and its variance; stratum-specific results must be interpreted with caution due to the greater variance associated with such estimates and the (typically) negative covariation between contiguous estimates. Results and figures generated in the course of analysis are provided more to support diagnosis and the use of stratified estimators than to encourage stratum-specific inference.

Saving the results

DARR 2.0 allows the analyst to save the results in comma-delimited (e.g., data.csv) or tab- or space-delimited (e.g., data.txt) formats. The comma-delimited format (.csv) is preferred as it can be read directly with typical spreadsheet applications without requiring an import utility. The resulting data file includes

⁸To paste the saved figure into a document, open or select document, place the cursor at desired location and press <ctrl>-v.

the original data, the results displayed previously (including everything needed to reconstruct the plot) and estimates of (1) stratum-specific capture probabilities, (2) for each mark group, the stratum-specific probabilities that marked individuals will be susceptible to recapture, and (3) the estimated variance-covariance matrix for the stratum-specific abundance estimates. DARR 2.0 can read in necessary data from a processed file for later analysis: the software will read in only what it needs automatically if such a file is selected at the start of the session.

Running another data set

After completing analysis on one data set, DARR 2.0 will offer the analyst the opportunity to analyze another data set. If the analyst selects “Yes”, DARR 2.0 will query the analyst for an input file, and the analysis will proceed as described above. If no other data are to be analyzed, and the analyst selects “No”, DARR 2.0 will exit and the MS-DOS window will close.

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Appendix A: Darroch’s (1961) stratified Peterson estimator

This appendix describes stratified mark-recapture experiments, and summarizes Darroch’s (1961) analysis for the simple case in which the recapture matrix is square, using the notation of (Seber, 1982).

In a stratified mark-recapture experiment, individuals bearing stratum-specific marks are released in each of s tagging strata, and marked and unmarked individuals sampled from the population in each of t recovery strata. Recaptured individuals, therefore, are identifiable (1) by the stratum in which they were marked and released and (2) by the stratum in which they were recaptured. Temporally stratified data may be arranged as

$$\begin{aligned} \mathbf{m} &= [m_1 \ m_2 \ \cdots \ m_s]^\prime \\ \mathbf{u} &= [u_1 \ u_2 \ \cdots \ u_t]^\prime \\ \mathbf{R} &= \begin{bmatrix} r_{11} & r_{12} & \cdots & r_{1t} \\ 0 & r_{22} & \cdots & r_{2t} \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & r_{st} \end{bmatrix} \end{aligned} \quad (\text{A.1})$$

where m_i is the number of individuals marked and released in tagging stratum i (herein referred to as “mark group i ”), u_j is the number of unmarked individuals captured in recovery stratum j , and r_{ij} is the number of individuals released in tagging stratum i that are recaptured in recovery stratum j . Note that an individual may be recaptured only once. Zeros below the main diagonal of \mathbf{R} occur because an individual can not be recaptured prior to its release; spatially stratified recapture data have no such constraint. Note that neither the number of tagging and recovery strata nor the boundaries of tagging strata and recovery strata need be identical; however, for many outmigrant trapping programs, tagging stratum i and recovery stratum i share the same start and end dates, which yields an equal number of tagging and recovery strata (i.e., $s = t$)⁹.

⁹Plante et al. (1998) and Bannehaka et al. (1997) further develop the stratified Peterson estimator for the general $s \times t$ case to obtain estimators for abundance in either tagging or recovery strata, depending on the parameterization and assumptions selected by the analyst. These methods have been implemented elsewhere (Arnason et al., 1996). DARR 2.0 focuses solely on the $s = t$ structure for simplicity of analysis and the ease with which patterns in the analyzed data may be interpreted.

The probability that a marked individual released in the i^{th} stratum will be recaptured in the j^{th} stratum is the joint probability that an individual released in stratum i will be susceptible to capture in stratum j , θ_{ij} , and the probability that an individual susceptible to capture in recovery stratum j will be captured, p_j . This “recapture probability” is defined as $\pi_{ij} = \theta_{ij}p_j$. Under the assumption that the group of marked and unmarked fish migrating in each stratum comprise a closed population (i.e., $\sum_j \theta_{ij} = 1$ for each tag group), estimates of the p_j allow expansion of the u_j into estimates of abundance of unmarked fish, n_j , according to $\hat{n}_j = \frac{u_j}{\hat{p}_j}$. (Variables and parameters marked with a “^” indicate estimated values.)

Darroch (1961) provides a maximum likelihood estimator for obtaining \hat{n}_j from data for which $s = t$ under the assumption that the rows of \mathbf{R} , $\{\mathbf{r}_i\}$, are mutually independent and that

$$\begin{aligned} \mathbf{r}_i &\sim \text{multinomial}(m_i, \{\boldsymbol{\pi}_i\}) \\ u_j &\sim \text{binomial}(n_j, p_j) \end{aligned} \quad (\text{A.2})$$

where $i = 1, 2, \dots, s$ and $j = 1, 2, \dots, t$ is an appropriate model of the data in Equation (A.2).

The analysis proceeds as follows. Reciprocals of capture probabilities are estimated as

$$\hat{\mathbf{b}} = \mathbf{R}^{-1}\mathbf{m} \quad (\text{A.3})$$

and used to expand counts of unmarked fish to estimates of total abundance according to

$$\hat{\mathbf{n}} = \mathbf{D}_u \hat{\mathbf{b}} \quad (\text{A.4})$$

where n_j is the estimated number of unmarked individuals that migrated past the trap in the j^{th} recovery stratum, \mathbf{R}^{-1} is the matrix inverse of the recapture matrix, and the notation \mathbf{D}_u indicates a diagonal matrix with elements of a vector (in this case \mathbf{u}) arranged along the diagonal and zeros elsewhere.

If individuals are captured, marked and released at one trap and recovered at a second (downstream) trap, total abundance is estimated by summing the estimated number of unmarked individuals susceptible to capture in each stratum and the number of individuals marked:

$$\hat{N} = \sum \hat{n}_j + \sum m_j. \quad (\text{A.5})$$

In smaller watersheds, often only one trap is deployed, and marked fish are transported a short distance upstream before release. In these cases, marked fish have already been counted and included in expansions during their initial capture as unmarked fish. Therefore,

$$\hat{N} = \sum \hat{n}_j. \quad (\text{A.6})$$

The estimated variance for the estimate of total abundance is obtained by summing the elements of the variance-covariance matrix for the stratum-specific abundance estimates:

$$\hat{V}(\hat{N}) = \sum_i^s \sum_j^t \widehat{cov}_{ij}(\hat{\mathbf{n}}). \quad (\text{A.7})$$

Note that $\hat{V}(\hat{N})$ is valid for both one-trap and two-trap experiments, since the number of marked fish is known exactly. The variance-covariance matrix for $\hat{\mathbf{n}}$ is approximated by

$$\widehat{cov}(\hat{\mathbf{n}}) \approx \mathbf{D}_n \boldsymbol{\Theta}^{-1} \mathbf{D}_\mu \mathbf{D}_m^{-1} (\boldsymbol{\Theta}')^{-1} \mathbf{D}_n + \mathbf{D}_n (\mathbf{D}_b - \mathbf{I}) \quad (\text{A.8})$$

where again \mathbf{D} indicate matrices with elements of the indicated vector along the diagonal and zeros elsewhere, and \mathbf{I} is an identity matrix. Elements of the vector $\boldsymbol{\mu}$ are calculated as $\mu_i = \sum_j (\hat{\theta}_{ij}/\hat{p}_j) - 1$. To estimate $\widehat{cov}(\hat{\mathbf{n}})$, requisite estimates are substituted into Eq (A.8), along with the matrix of estimated migration probabilities, $\hat{\boldsymbol{\Theta}}$, estimated as

$$\hat{\boldsymbol{\Theta}} = \mathbf{D}_m^{-1} \mathbf{R} \mathbf{D}_b. \quad (\text{A.9})$$

Note that \hat{N} is approximately unbiased for large m (Darroch, 1961); if \hat{N} is biased, $\hat{V}(\hat{N})$ calculated with Eq (A.8) actually estimates the mean squared error of \hat{N} . Because the estimates of abundance for pairs of contiguous strata generally covary negatively, $\hat{V}(\hat{N})$ may be substantially less than the variance estimated for any individual stratum (diagonal elements of $\widehat{cov}(\hat{\mathbf{n}})$).

In the preceding analysis, it is assumed that the population is closed and all marked individuals are ultimately susceptible to recapture (i.e., $\sum_j \theta_{ij} = 1$ for all i). If mortality rates are greater than zero, but constant across all strata, the abundance estimates are correct only to within an unknown scaling factor based on the probability of survival (Darroch, 1961). Accounting for variable (relative) survival among strata requires

analysis of data with unequal numbers of tagging and recovery strata (Darroch, 1961; Plante et al., 1998). At least three sampling times or locations are required to estimate absolute survival rates (Arnason, 1973). Note that this issue differs subtly from the issue of tagging mortality. For the latter case, estimates of mortality of marked individuals obtained by holding marked individuals for observation may be used to adjust the expected number of marked individuals in the population prior to analysis.

Conditions for failure of the Darroch estimator

The Darroch estimator requires that at least some marked individuals are susceptible to recapture in the same stratum in which they were released (i.e., $\theta_{ij} \neq 0$ for all $i = j$) (Darroch 1961). This is known to be true if during the experiment, at least one “immediate” recapture is observed for each mark group. If this is not the case, \mathbf{R} is singular, which precludes solving Eq (A.4). Even when immediate recaptures are observed, low numbers of immediate recaptures can reduce the precision of estimates and yield estimates that are highly sensitive to sampling error in the data (Darroch, 1961).

Note also that the elements of $\hat{\mathbf{p}}$ are not constrained to the interval $[0, 1]$ and therefore it is possible to obtain inadmissible estimates of capture probability (i.e., p_j that are < 0 or > 1). Inadmissible \hat{p}_j might arise as a consequence of violations of model assumptions (e.g., unequal mortality among mark-groups, or variability in capture probability during a given stratum among fish bearing different marks). Inadmissible \hat{p}_j might also arise as a consequence of sampling error that causes substantial deviation in the data from expectations for the distribution of recaptures. Recoveries collected from small mark-groups are more likely to include substantial sampling error, that, even when model assumptions hold and analysis is technically possible, may cause inadmissible estimates.

Appendix B: Rules for aggregating stratified mark-recapture data for analysis

Direct application of the Darroch estimator to data obtained from small populations may be impossible or ill-advised due to consequences of small sample sizes, particularly for populations that exhibit substantial migration among strata. In many cases, however, it is possible to aggregate the data in such a way that the data become amenable to analysis (Darroch, 1961; Schwarz and Taylor, 1998). In this appendix, I outline the DARR 2.0 algorithm to identify structures in stratified data that hinder or prevent analysis and to eliminate these structures by aggregation of strata. Aggregation consists of converting a $s \times t$ (where $s = t = k$) recovery matrix \mathbf{R} to a $(s - 1) \times (t - 1)$ matrix by combining columns and rows of \mathbf{R} that correspond to the i^{th} and $(i + 1)^{\text{th}}$ tagging and recovery strata and combining the corresponding elements of \mathbf{m} and \mathbf{c} to reduce these vectors from k to $(k - 1)$ elements (Appendix C). Doing so reduces the number of discrete strata in the mark-recapture data and usually (but not necessarily) reduces the rank of \mathbf{R} , that is the number of linearly independent rows of \mathbf{R} . The algorithm is designed to retain as much of the information contained in the original data as possible. Strict adherence to maintaining a square recapture matrix by aggregating coincident release and recovery strata has been selected for simplicity of analysis and provides some advantage in the ease with which patterns in the final analysis may be interpreted.

Step 1: In this step, \mathbf{R} is shifted, if necessary, to obtain an \mathbf{R} with a dominant main diagonal. If the sum of immediate recaptures (i.e., values on the main diagonal of \mathbf{R}) is less than the sum of delayed recaptures (i.e., values above the main diagonal of \mathbf{R}), recovery strata are shifted “forward” in time, with entries for the first recovery stratum combined with the second in both \mathbf{R} and \mathbf{u} . Zeros are appended to \mathbf{R} and \mathbf{u} after the final recovery stratum as needed to maintain $s = t$.

Step 2: In this step, the data are aggregated to produce a non-singular \mathbf{R} . All strata that lack an immediate recapture are pooled with neighboring strata so that no zeros remain along the main diagonal of the aggregated recapture matrix.

Step 3: In this step, the data are further aggregated to eliminate strata with sufficiently few immediate re-

captures to compromise the accuracy and precision of the abundance estimate. The Darroch (1961) estimator solves a system of linear equations described by the recapture matrix \mathbf{R} (e.g., Eq (A.2)). The condition number of \mathbf{R} provides a measure of how sensitive the solution of this system of linear equations is to sampling error in the matrix entries, and thus can be used to examine what entries in \mathbf{R} are most likely to compromise the accuracy of the stratum-specific abundance estimates. A small condition value for \mathbf{R} suggests that solutions to Eq (A.4) are robust. Aggregation is judged necessary whenever the condition number of \mathbf{R} exceeds the mean number of immediate recaptures. This flexible threshold criterion reflects the dependence of the condition number on the values in \mathbf{R} .

The condition number of \mathbf{R} is the ratio of the largest to the smallest singular value in the singular value decomposition of \mathbf{R} . Increasing the smallest singular value, i.e., the denominator, is only one of two ways to reduce the condition number. The magnitude of singular values is related to the magnitude of entries along the main diagonal, such that small singular values tend to be associated with small matrix entries. Therefore, to select a stratum for pooling, the condition number and singular values are calculated for all possible matrices resulting from pooling one stratum, and the case that yields the greatest reduction in condition as a consequence of increasing the minimum singular value is retained. As a consequence, this criterion favors aggregation of strata with few recaptures over those with many. If multiple strata satisfy this criterion, the stratum nearest the start or the end of the data is aggregated, with preference for aggregating the earliest stratum in the case of identical options at the start or end of the data.

Step 3 is iterated until a condition threshold specific to the data is no longer exceeded. Since the condition number of \mathbf{R} is related to the range of entries in \mathbf{R} , especially along the main diagonal, a fixed threshold can overaggregate data that include on large numbers of recaptures and underaggregate data that include few recaptures. Simulations indicate that using the mean value of (non-zero) entries along the main diagonal of \mathbf{R} as the condition threshold yields consistent behavior of the estimator across a wide range of abundances and capture probabilities (E. P. Bjorkstedt *in prep.*). Note that Step 3 is a special case of Step 2, since the condi-

tion number of a singular matrix is infinity.

Step 4: In this step, the data are further aggregated to eliminate any strata for which an inadmissible estimate of capture probability is obtained. If analysis yields any inadmissible \hat{p}_j , the stratum for which \hat{p}_j falls furthest outside the interval $[0, 1]$ is aggregated with a contiguous stratum, and the newly aggregated data reanalyzed and examined for inadmissible \hat{p}_j . This step is iterated until all capture probabilities fall between zero and one, and the resulting data set is retained for final analysis.

Appendix C: Aggregation scheme and consequences for model structure

This appendix (1) illustrates the algorithm used to aggregate stratified mark-recapture data by combining a pair of contiguous strata, and (2) briefly outlines the consequences of such aggregation for model structure and relevant assumptions. Consider the mark-recapture data

$$\begin{aligned} \mathbf{u} &= [u_1 \ u_2 \ u_3 \ u_4]' \\ \mathbf{m} &= [m_1 \ m_2 \ m_3 \ m_4]' \\ \mathbf{R} &= \begin{bmatrix} r_{11} & r_{12} & r_{13} & r_{14} \\ 0 & r_{22} & r_{23} & r_{24} \\ 0 & 0 & r_{33} & r_{34} \\ 0 & 0 & 0 & r_{44} \end{bmatrix} \end{aligned} \quad (\text{C.1})$$

for which stratum 2 has been selected for aggregation according to one of the criteria described in the Appendix B. If $r_{3.} < r_{1.}$, where $r_{i.} = \sum_j r_{ij}$, stratum 2 is combined with stratum 3, which yields

$$\begin{aligned} \mathbf{u}^* &= [u_1 \ (u_2 + u_3) \ u_4]' \\ \mathbf{m}^* &= [m_1 \ (m_2 + m_3) \ m_4]' \\ \mathbf{R}^* &= \begin{bmatrix} r_{11} & (r_{12} + r_{13}) & r_{14} \\ 0 & (r_{22} + r_{23} + r_{33}) & (r_{24} + r_{34}) \\ 0 & 0 & r_{44} \end{bmatrix} \end{aligned} \quad (\text{C.2})$$

Conversely, if $r_{3.} > r_{1.}$, stratum 2 is combined with stratum 1, which yields

$$\begin{aligned} \mathbf{u}^* &= [(u_1 + u_2) \ u_3 \ u_4]' \\ \mathbf{m}^* &= [(m_1 + m_2) \ m_3 \ m_4]' \\ \mathbf{R}^* &= \begin{bmatrix} (r_{11} + r_{12} + r_{22}) & (r_{13} + r_{23}) & (r_{14} + r_{24}) \\ 0 & r_{33} & r_{34} \\ 0 & 0 & r_{44} \end{bmatrix} \end{aligned} \quad (\text{C.3})$$

Choosing to combine a selected stratum with the neighboring stratum that has fewer recaptures prevents run-away aggregation of the data set by a single stratum with an increasingly large number of recoveries and thus favors retaining as many distinct strata as possible.

To illustrate the consequences of aggregating data for model structure and potential bias in the course of estimating abundance, I consider the simplest general case, consisting of four strata, of which the second and third are to be pooled according to Equation (C.3). Quantities and parameters in the aggregated data are indicated by “*” and their indices will reflect the structure of the aggregated data. After pooling, the number of marked fish released in each stratum is

$$\mathbf{m}^* = \begin{bmatrix} m_1^* \\ m_2^* \\ m_3^* \end{bmatrix} \quad (\text{C.4})$$

where $m_1^* = m_1$, $m_2^* = m_2 + m_3$, and $m_3^* = m_4$.

$$\mathbf{n}^* = \begin{bmatrix} n_1^* \\ n_2^* \\ n_3^* \end{bmatrix} = \begin{bmatrix} n_1 \\ n_2 + n_3 \\ n_4 \end{bmatrix} \quad (\text{C.5})$$

is the analogous expression for the numbers of unmarked fish susceptible to capture during each stratum after aggregation.

The expectation of the aggregated recapture matrix \mathbf{r}^* is

$$E[\mathbf{r}^*] = \begin{bmatrix} m_1\pi_{11} & m_1(\pi_{12} + \pi_{13}) & m_1\pi_{14} \\ 0 & m_2(\pi_{22} + \pi_{23}) + m_3\pi_{33} & m_2\pi_{24} + m_3\pi_{34} \\ 0 & 0 & m_4\pi_{44} \end{bmatrix} \quad (\text{C.6})$$

and the expected catch of unmarked fish is

$$E[\mathbf{u}^*] = \begin{bmatrix} n_1 p_1 \\ n_2 p_2 + n_3 p_3 \\ n_4 p_4 \end{bmatrix}. \quad (\text{C.7})$$

To write $E[\mathbf{R}^*]$ and $E[\mathbf{u}^*]$ in terms of aggregated parameters, it is useful to define the recapture probability¹⁰ for each aggregated stratum as a weighted average of the recapture probabilities for the corresponding original strata. For example,

$$\pi_{22}^* = \frac{m_2(\pi_{22} + \pi_{23}) + m_3\pi_{33}}{m_2 + m_3}. \quad (\text{C.8})$$

which corresponds to

$$E[r_{22}^*] = m_2(\pi_{22} + \pi_{23}) + m_3\pi_{33}. \quad (\text{C.9})$$

Likewise, the combined pool of unmarked fish experience a probability of capture during the aggregated period that is a weighted average of capture probabilities during the original strata, e.g.,

$$p_2^* = \frac{n_2 p_2 + n_3 p_3}{n_2 + n_3}. \quad (\text{C.10})$$

which corresponds to

$$E[u^*] = n_2 p_2 + n_3 p_3. \quad (\text{C.11})$$

With these and analogous definitions, Eqs (C.6) and (C.7) may be written as

$$E[\mathbf{R}^*] = \begin{bmatrix} m_1^* \pi_{11}^* & m_1^* \pi_{12}^* & m_1^* \pi_{13}^* \\ 0 & m_2^* \pi_{22}^* & m_2^* \pi_{23}^* \\ 0 & 0 & m_3^* \pi_{33}^* \end{bmatrix}, \quad (\text{C.12})$$

and

$$E[\mathbf{u}^*] = \begin{bmatrix} n_1^* p_1^* \\ n_2^* p_2^* \\ n_3^* p_3^* \end{bmatrix}, \quad (\text{C.13})$$

¹⁰Recall that the probability that an individual marked in one stratum will be recaptured in that or a subsequent stratum is a joint probability composed of the probability that the individual will be susceptible to capture in a given stratum and the probability that susceptible individuals will be captured during that stratum.

respectively. Note that, although the $\{\mathbf{r}_i^*\}$ are no longer necessarily distributed multinomially, nor are the $\{u_j^*\}$ necessarily distributed binomially, the model that will be assumed for the aggregated data is

$$\begin{aligned} \mathbf{r}_i^* &\sim \text{multinomial}(m_i^*, \{\boldsymbol{\pi}_i^*\}) \\ c_j^* &\sim \text{binomial}(n_j^*, p_j^*) \end{aligned} \tag{C.14}$$

where $i = 1, \dots, s^*$, $j = 1, \dots, t^*$, and $s^* = t^* = k^*$ is the number of strata in the aggregated data, and mutual independence of the $\{\mathbf{r}_i^*\}$ is again assumed. As alluded to previously, estimating parameters for Eq (C.14) requires a revised set of assumptions: capture probability must now be assumed to be constant throughout each combined stratum, even though capture probability may have differed among the original strata. Each aggregation of strata leads to a simpler model with increasingly restrictive assumptions.

The use of Eq () can yield bias in the resulting estimate of abundance, and the consequences of aggregation for estimator bias are considered elsewhere in greater detail (Bannehaka et al., 1997; Schwarz and Taylor, 1998, A. N. Arnason, C. W. Kirby, and C. J. Schwarz, *unpublished ms.*, E. P. Bjorkstedt *in prep.*).